Larval ontogeny and survivorship of eastern tent caterpillar colonies

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Abstract. This study documents spatial and temporal variation in mortality in a population of 100 naturally-occurring colonies of eastern tent caterpillars (*Malacosoma americanum*). Predation took the heaviest toll on colonies, while very few colonies were significantly affected by disease. Predation by invertebrates was widespread, but far less catastrophic than vertebrate (avian) predation. Predation and disease incidence varied considerably among study sites and among larval instars. Early-instar colonies suffered the greatest rates of mortality, with 30% of the colonies destroyed by the 3rd-4th instar. Spatial and some temporal variation in mortality and morbidity was stochastic. Temporal variation also arises from individual phenology, as a consequence of larval development and its effects on defense- and foraging-related character suites. The social behaviors of eastern tent caterpillars are discussed in terms of a character suite collectively enhancing larval defense and nutrition, resulting in rapid growth to decreasingly-vulnerable age classes.

KEY WORDS: Eastern tent caterpillar, Lepidoptera, Lasiocampidae, *Malacosoma americanum*, mortality, predation, survivorship

INTRODUCTION

The life of a caterpillar is characterized by a tradeoff between behaviors enhancing growth and development, and those reducing risk of mortality from predators, parasites, and disease. It has long been understood that behavioral, morphological, and physiological characters that play defensive and nutritional roles may evolve in response to selective pressures implicit in this tradeoff. In some species, this tradeoff is manifested as selection of feeding sites well-protected from predators but sub-optimal in leaf nutritional quality or thermal regime (Stamp and Bowers 1988, Haukioja 1993, Stamp 1993). Defensive evolutionary responses may include specialized structures (setae, spines, tubercles, etc.), allelochemicals (secretion or regurgitation of toxic substances), and/or somatic modifications (crypsis and mimicry) (see examples in Owen 1980). Responses to nutritional needs are not as obvious, but include behaviors facilitating location of profitable food and physiological adaptations to detoxify and metabolize certain hosts.

It is obvious that lepidopteran larvae experience the greatest mortality rates in the early immature stages, and it is equally obvious that factors contributing to mortality are numerous, and vary in intensity spatially and temporally (see Heinrich 1993, Montllor and Bernays 1993, Reavey 1993). Spatial and temporal variation in mortality factors is commonly perceived as

the joint product of stochasticity and a fluctuating environmental mosaic. Another important dimension to this variation, however, is simply ontogenetic change. Ontogenetic changes include growth as well as changes in shape, color, and physiology. Such changes are often dramatic in caterpillars, many of which exhibit striking modifications of size, color, and armature with each instar, along with changes in behavior (e.g., Owen 1980, Booth 1990, Heinrich 1993, Reavey 1993).

In this paper I document spatial and temporal survivorship patterns in a population of eastern tent caterpillars, *Malacosoma americanum* (Fabricius) (Lepidoptera: Lasiocampidae). This study departs from typical survivorship analyses by focusing on *colony* survivorship rather than survivorship of individuals. A colony-level focus is useful because this species is highly social, with well-integrated cooperative behaviors that include nest (tent) construction and recruitment-based foraging (e.g., Fitzgerald and Peterson 1983; Fitzgerald 1993; see below). Individual survivorship is closely tied to that of the group, and isolated individuals experience extremely high rates of mortality (Shiga 1976, Sedivy 1978, Robison 1993).

EASTERN TENT CATERPILLAR LIFE HISTORY

Eastern tent caterpillars spend about 10 months of the year in the egg stage. The eggs are deposited as closely-packed masses numbering between 100 and 300 near the twig-tips of their hosts, commonly black cherry (*Prunus serotina*) and apple (*Malus* spp.). Each egg mass is covered with a frothy accessory-gland secretion called spumaline. Oviposition time ranges from late winter to early spring in the southern part of the species range to late spring in the northern part; the caterpillars overwinter as pharate larvae within the eggs. Eclosion the following spring is tightly correlated with budbreak of the host tree; this species is thus among the earliest insects to emerge in the spring (Stehr and Cook 1968).

The larvae migrate soon after eclosion to a more or less centrally-located region of the host tree where they begin to construct their communal tents in the crotches of large branches. Each group feeding bout, of which there are three to four per day, is immediately preceded by a characteristic period of silk-spinning behavior which contributes to tent construction (Fitzgerald and Willer 1983, Fitzgerald et al. 1988). Development following eclosion proceeds rapidly under favorable environmental conditions; accelerated growth is achieved by thermoregulatory basking behavior utilizing the communal tent as a basking or shading platform (Knapp and Casey 1986, Casey et al. 1988, Fitzgerald 1993).

Instar number is typically six. Under optimal conditions the larval stage is completed in five to six weeks, so the caterpillars grow at an approximate rate of one instar per week, during which time they grow from about 2mm upon eclosion to about 5cm upon pupation - a striking growth rate of about a centimeter per week on average. The pupal stage lasts approximately 10 days, after which the adults emerge, mate, oviposit, and die often within the space of a few days (Stehr and Cook 1968).

Table 1. Larval instars and sampling dates for 100 eastern tent caterpillar colonies monitored through the 1990 developmental season in Clarke County, Georgia: Eclosion = hatching, CP1-4 = census points 1-4, Post-larval = colony abandonment and pupation.

Census Dates (1990)	Instars	Designation
5-7 March	1	Eclosion
14-15 March	1-2	CP1
27-29 March	3-4	CP2
4-6 April	4-5	CP3
20-22 April	5-6	CP4
28-30 April	N/A	Post-larval

METHODS

One hundred overwintering eastern tent caterpillar egg masses from five site localities in Clarke County, Georgia, separated by one to ten km, were identified for observation in January 1990. These egg masses were found on the favored hostplant, black cherry (*P. serotina*), and were recognized as current-generation by the fresh state of their spumaline coating (Stehr and Cook 1968). The egg masses were monitored closely for eclosion, which occurs synchronously with hostplant bud-break in a given locality (Stehr and Cook 1968), after which all colonies were censused at 1-2 week intervals throughout the larval developmental period (Table 1). This period is approximately six weeks long on the Georgia piedmont, during which time the larvae grow through six instars.

Because of the tendency of eastern tent caterpillars to rest within their tents between feeding bouts, it was not possible to accurately census caterpillars within colonies. Thus, the focus of this study was on *colonies* as demographic units. Colonies were evaluated using six descriptors at each census point: (1) intact, (2) predator destroyed, (3) predator damaged, (4) disease destroyed, (5) disease damaged, and (6) abandoned/merged. Intact colonies were evaluated for evidence of disease and predation, and were considered "damaged" if it could be ascertained that a large proportion (appx. 25%) of individuals were missing and/or the tent displayed evidence of predator damage; this cutoff level is necessarily arbitrary. Diseased colonies were readily identifiable, since diseased and parasitized individuals appear stunted relative to healthy larvae (e.g., Bucher 1957), giving the appearance of a multiple-instar colony. Also, dead and dying caterpillars are commonly found on the tent surface and the symptoms of the main pathogen classes are characteristic (Witter and Kulman 1972; see below). The state of the tent was also used to determine the fate of "missing" colonies. Colony destruction was identified as (vertebrate) predator-induced by the presence of tent damage, or disease-induced by the presence of dead larvae in and on the tent (see discussion below). Mortality in colonies decimated by predators is considered to be complete because solitary or small bands of caterpillars, especially in the early instars, are highly unlikely to survive to pupation (e.g., Shiga 1976, 1979).

Finally, tents were identified as abandoned/merged if they were structurally intact but contained no larvae. This category was distinguishable from colonies decimated by predation away from the tent because in the latter case remnant caterpillars are
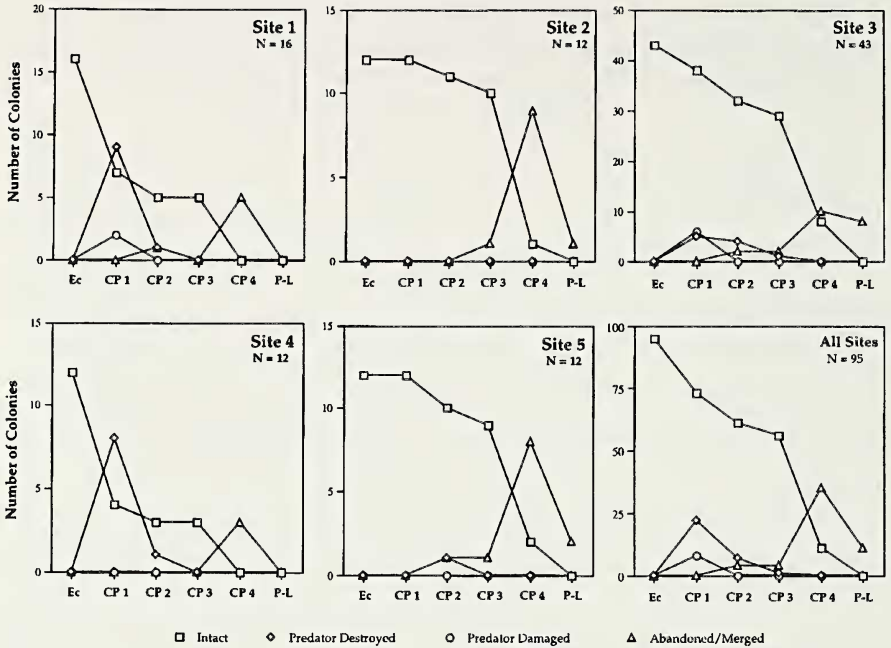
Figure 1. Survivorship and predation rates for eastern tent caterpillar colonies from five field sites in Clarke County, Georgia, spring 1990. Colony status was evaluated at each of six points: Ec = Eclosion, CP1-4 = larval census points 1-4, P-L = Post-larval. "Predator damaged" indicates significant ($\approx$ 25%) larval mortality with physical evidence of predation; "predator destroyed" indicates complete colony destruction with evidence of predation. "Abandoned/Merged" indicates tent abandonment or colony merging. Colony mortality rates are spatially and temporally variable: the spatial variation is attributed to chance, while the temporal variation reflects differential age-dependent vulnerability. The concentration of predator-induced colony damage and destruction in early larval instars is characteristic of an early-instar vulnerability window (see text).

nearly always present, while tent abandonment tends to be complete. Tent abandonment is not uncommon in mid-to-late instars, and stems from three causes: (1) exhaustion of food, (2) colony merging (Fitzgerald and Willer 1983, Costa and Ross 1993), or (3) dissolution of the social group as larvae leave to seek solitary pupation sites (Stehr and Cook 1968, Fitzgerald 1993).

Results and Discussion

The fates of these colonies illustrates the relative importance of different mortality factors affecting subdivided caterpillar populations. Five of the 100 colonies apparently failed to eclose. It is likely that these egg masses experienced a high incidence of disease or inviability such that the few emerging caterpillars were killed; egg parasitism is readily identifiable (Witter and Kulman 1972, Darling and Johnson 1982) and did not account

Table 2. Incidence of disease for 100 naturally-occurring eastern tent caterpillar colonies monitored in Clarke County, Georgia, in the spring of 1990. Most colonies exhibited some diseased individuals ("low level"), while few were severely affected. Disease-ravaged colonies are classified as "disease damaged" ($\approx$ 25% larval mortality) or "disease destroyed" ($\approx$ 100% larval mortality). By the end of the developmental season (CP3-CP4), all intact colonies lost some individuals to disease. The severely-affected colonies suffered from nuclear polyhedrosis virus.

	Eclosion	CP 1	CP2	CP3	CP4
Low level	0	0	58	56	11
Damaged	0	0	3	2	0
Destroyed	0	0	1	0	0

for complete eclosion failure. In the remaining 95 colonies, predation was the most significant cause of mortality. Colony survivorship and predation-related mortality data are presented for the five study sites individually and summarized for all sites (Fig. 1). Data for disease are presented in summary form only because of low incidence (Table 2). Climatic factors did not contribute to mortality in this population; this is typical of regions such as the Georgia piedmont where springtime freezes are rare, but climate is likely to play an important role in colony mortality at higher elevations and latitudes. The following sections discuss disease and predation within the context of spatial and temporal variation and larval susceptibility.

Disease

Like other caterpillar species, *M. americanum* is attacked by a variety of pathogens. The most common of these are the nuclear polyhedrosis viruses and some *Clostridium* and *Bacillus* bacteria (Bucher 1957, 1961, Stehr and Cook 1968, Witter and Kulman 1972). These pathogens are distinctive in their symptoms, and moribund larvae commonly expire directly on the tent surface. The viral disease tends to internally liquefy the larvae, which often simply disintegrate, leaving parts of the body clinging to the substrate by one or two prolegs. The bacterial disease is, in contrast, manifested by desiccation and shrinking of the body. The incidence of these and other pathogens is highly variable, at times reaching epidemic proportions (though not in this study population). Nearly all colonies in the present study exhibited a few diseased individuals, but only six colonies from three sites experienced significant disease mortality, and only a single colony was completely destroyed (Table 2).

Predation

Predation levels varied considerably among study sites, ranging from negligible (sites 2 and 5) to high (sites 1 and 4). Figure 1 shows that most predator-induced colony mortality occurred by the first census point (1st-2nd

instar caterpillars) and declined with time. Overall mortality was approx. 30% (n = 29 colonies) by the second census point (3rd- 4th instar caterpillars). Tent damage points to a high incidence of vertebrate predation in this population. Most completely-destroyed colonies exhibited the circular holes and tears indicative of avian predators, and in two instances parid birds (*Parus caroliniana* and *P. bicolor*) were observed attacking small tents. Invertebrate predation was widespread but consistently low in frequency, though it was not possible to quantify invertebrate predation rate. Some individuals in most colonies were parasitized by tachinid flies, but no colony was completely destroyed by invertebrate predators. Thus, invertebrate predators were responsible for widespread low-level individual mortality, while vertebrate predation tended to be far more devastating to colonies. However, attack by a vertebrate predator may increase the risk of invertebrate predation by breaching the tent; for example, ants of the genus *Pheidole* were observed in great numbers within one tent torn by a bird and may have been responsible for completing the destruction begun by the bird.

The absence of complete colony destruction by invertebrate predators is not surprising, since most of these predators (e.g., ants and pentatomid bugs) are closer to their prey in relative body size than vertebrate predators and experience greater prey handling time. However, invertebrate predators vary in destructive potential. Casey et al. (1988) reported disruption of some field experiments due to repeated predation by *Polistes* wasps, and Knapp and Casey (1986) reported that 51% of tent caterpillars brought into the laboratory died of tachinid parasitoids.

While at least 56 species of birds have been reported as predators of tent caterpillar larvae and pupae (Witter and Kulman 1972), few birds will regularly feed upon mature larvae, presumably due to setae and toxicity. Young larvae, however, are poorly defended and relatively conspicuous, and it is likely that insectivorous birds are responsible for much early-instar mortality. This is especially likely since the temporal occurrence of young colonies of eastern tent caterpillars coincides with the spring migration and breeding season of many insectivorous birds in eastern North America (Witter and Kulman 1972).

Larval vulnerability

This study illustrates spatial and temporal variation in mortality factors affecting eastern tent caterpillar populations. Spatial variation is attributed largely to chance, due to the stochastic nature of "discovery" of population patches by pathogens and predators. Temporal variation behaves in a similar fashion on a scale of years as pathogen and predator populations, as well as climatic conditions, fluctuate.

Another form of temporal variation does not stem from stochastic factors so much as from larval phenology itself. Ontogenetic changes (somatic, behavioral, and physiological) are both cause and effect of the shifting vulnerability to mortality factors that individuals experience (Booth 1990). Costa and Pierce (1996) suggest that age-related behavioral and somatic

polymorphism in caterpillars may be best understood within the context of an early-instar vulnerability window arising from a lag time between eclosion and maturation of physical, behavioral, and physiological defensive characters.

Gregarious caterpillars have the problem of apparency in all instars, and gregariousness is especially problematic in early instars when defensive suites are least effective and the threat of predators and parasites is greatest. Relative body size is an important determinant of range of predators and of anti-predator defenses and avoidance strategies (see reviews by Bowers 1993, Heinrich 1993, Montllor and Bernays 1993, Reavey 1993). This is true of *M. americanum*, which exhibits increasingly effective structural, chemical, and behavioral defenses against predators as larvae age (Sullivan and Green 1950, Tilman 1978, Evans 1983).

If larval size and age are key determinants of vulnerability, enhanced growth rate is a simple means of diminishing duration of vulnerable age classes. An effect of the social behavior of eastern tent caterpillars is rapid growth, a phenomenon all the more impressive in light of the fact that these caterpillars are active during the spring and experience large fluctuations in temperature in many parts of the species range. Casey et al. (1988) demonstrated that the rapid growth rate of this species is attributable to behavioral thermoregulation: the massed caterpillars utilize their tent as a basking platform, raising their body temperatures as much as 20° C above ambient. This improves metabolism and enables caterpillars to consume more food per foraging bout (Casey et al. 1988, Joos et al. 1988). Behavioral thermoregulation is integrated with other aspects of tent caterpillar social biology as well, which collectively contribute to growth. For example, eastern tent caterpillars cooperate in the location of high-quality food through elective recruitment to young, newly-expanded foliage (Fitzgerald and Peterson 1983, Peterson 1987), and their structural and group-behavioral defenses help repel predators and parasitoids when feeding and basking (Myers and Smith 1978, Peterson et al. 1987).

The importance of nutritional quality and defense to caterpillar growth has been established for other gregarious Lepidoptera (Stamp and Bowers 1990a,b; Montllor and Bernays 1993; Reavey 1993, Stamp 1993). Sociality in eastern tent caterpillars encompasses a suite of characters that collectively bear on group defense and resource use, and this leads to rapid growth through the larval vulnerability window (Costa and Pierce 1996). In other words, rapid growth is *itself* a form of defense.

To conclude, the caterpillar's dilemma is a tradeoff between behavior geared for growing large quickly and the risks this behavior incurs, giving rise to the rich morphological and behavioral diversity of caterpillars. Ontogenetic change in physiology, morphology, and behavior is an important contributor to changes in the intensity of selective pressures experienced by organisms in general and caterpillars in particular, because these changes are both cause and effect of temporal variance in selective pressures. In lepidopteran larvae, the vulnerability window created by this variance is

centered on the earliest larval instars such that individuals (and colonies) experience a high probability of mortality in the early instars that declines through time. Larval gregariousness, or sociality, involves a character suite that may mitigate vulnerability through group effects improving defense, nutrition, and selection of thermal niche (Cornell et al. 1987, Vulinec 1990, Stamp and Bowers 1990a,b, Bowers 1993), which in turn enhance growth and development (Casey et al. 1988, Joos et al. 1988, Stamp 1990b, 1991). The eastern tent caterpillar population in this study exhibits significant early-instar mortality and negligible mid- to late-instar mortality. Colonies surviving to mid-instars are more likely to survive to pupation, a pattern that may be described in terms of mortality probability as an inverse function of larval age. Temporal variance in mortality factors is thus as much a product of development as of stochasticity, and sociality in this species is important to age-dependent larval vulnerability through effects on caterpillar phenology.

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